

NIMIOKOALA GEN. NOV. (MARSUPIALIA, PHASCOLARCTIDAE) FROM
RIVERSLEIGH, NORTHWESTERN QUEENSLAND, WITH A REVISION OF
LITOKOALA

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The early to middle Miocene phascolarctid *Nimiokoala greystanesi* gen. et sp. nov. is described from Riversleigh, northwestern Queensland. *Nimiokoala* sp. is recognised from a late Oligocene deposit in South Australia. The complex molar morphology and plesiomorphic basicranial morphology of *Nimiokoala* are indicative of a more diverse infraorder of phascolarctomorphians. Similarities in molar morphology between *Nimiokoala* and ektopodontids are noted and may reflect similar ecological niche. *Litokoala kanunkaensis* is described from the Miocene of Riversleigh extending its range and distribution. Cladistic analyses of dental characters of all living and extinct taxa support the intrafamilial relationships proposed by Woodburne et al. (1987a). *Litokoala* is identified as the sister group of the modern genus and *Nimiokoala* is most closely related to the *Litokoala*/*Phascolarctos* clade. □ *Phascolarctidae*, *Nimiokoala*, *Litokoala*, *Oligocene*, *Miocene*, *Riversleigh*.

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A partial skull, representing a small, highly specialised phascolarctid was collected from Boid Site East, System B deposits (Archer et al., 1989; 1991), Riversleigh, northwestern Queensland. Based on a superficial analysis of dental morphology, the skull was incorrectly figured by Archer et al. (1991) as a new species of the Miocene phascolarctid *Litokoala*. Two species of *Litokoala* were known: *L. kutjamarpuensis* (Stirton et al., 1967) from the Kutjamarpu Local Fauna, Wipajiri Formation, Lake Ngapakaldi, South Australia (known from a single upper molar) and *L. kanunkaensis* (Springer, 1987) from the Kanunka North Local Fauna, Etadunna Formation, South Australia (known from 2 isolated teeth and some molar fragments).

N. greystanesi gen. et sp. nov. is similar to *Litokoala* but its generic separation is substantiated by comparison with new material (an M³ and a lower dentition) of *L. kanunkaensis* from System C (Archer et al., 1989; 1991) at Riversleigh. A further new species of *Nimiokoala* is recognised from South Prospect B Locality, Lake Namba, Frome Downs Station, South Australia.

The moderate abundance of *N. greystanesi* in Riversleigh deposits contrasts with the paucity of material of other phascolarctids which are known from isolated teeth or, at best, dentitions. This paper describes dentition of the new genus and analyses phascolarctid phylogeny based on dental characters.

Suprageneric nomenclature follows Aplin &

Archer (1987). Dental terminology follows Archer (1978b) except that what was then understood to be the hypocone of upper molars is now accepted to be the metaconule (Tedford & Woodburne, 1987). Cheek tooth homology is that proposed by Luckett (1993). Biostratigraphic nomenclature follows Woodburne et al. (1993), Archer et al. (1989) and Archer et al. (1991). Specimens referred to are housed in the following repositories: Queensland Museum (QMF), South Australian Museum (SAMP), University of California at Riverside (UCR). Measurements were made using a Wild M5 microscope with digital length measuring set.

SYSTEMATICS

Order DIPROTODONTIA Owen, 1866
Suborder VOMBATIFORMES Woodburne, 1984
Infraorder PHASCOLARCTOMORPHIA
Aplin & Archer, 1987
Family PHASCOLARCTIDAE Owen, 1839

Nimiokoala gen. nov.

TYPE SPECIES. *Nimiokoala greystanesi* sp. nov.

ADDITIONAL SPECIES. *Nimiokoala* sp.

DIAGNOSIS. *Nimiokoala* differ from all other phascolarctids in: being smaller (except species

of *Litokoala*); having a large, cusped parastyle which is pyramidal in occlusal view (except *Litokoala kutjampensis*); a well-developed, crescentic paracone and neometaconule on M^{1-4} , the latter of which is double cusped in the more posterior molars; a more reduced metacone and metaconule on M^4 and a more rounded posterior margin of that tooth.

Robust, ridge-like crenulations; strong posterobuccal ridges from the apices of the protocone and metaconule; a discontinuous neometaconule subdivided into two or more parts and a (variably) discontinuous paracone; a posterolingual cusp on P_3 ; a well-developed posterolingual crest from the apex of the protostylid on M_1 ; a weaker metastylid; a well-developed neomorphic cuspid occupying the trigonid basin between the metaconid and protoconid on $M_{2.4}$; an anterobuccally directed pre-entocristid (as opposed to anterolingually directed in other phascolarctids); a well-developed cusped entostylid ridge; and a more posterobuccally directed postprotostylid cristid.

Nimiokoala greystanesi differs from *Koobor* in: being higher crowned; lacking the bicusped P^3 ; having strong posterolingual paracristae and posterolingual metacristae; having a protostyle; and in having reduced styler cusps and from *Madakoala* in: being higher crowned; more crenulated; in having a more cusped, isolated posterolingual cusp on P^3 and in lacking the lingual cingular ridge of that tooth (in *M. sp. cf. M. wellsii*); having wider, less elongate upper molars; a more buccal junction of the premetacristae and postparacristae; a well-developed protostyle; relatively smaller buccal surfaces of the paracone and metacone; lacking the transverse connection between the metacone and metaconule on M^4 ; having a less elongate P_3 that consists of three main apices (as opposed to four in *Madakoala*), a small posterolingual cuspid and a proportionately larger, more isolated posterobuccal cusp on that tooth; lacking the well-developed buccal and lingual crests from the main apices of P_3 ; having a larger, more cusped protostylid on M_1 ; a more lingually situated protoconid and a more lingual junction of the cristid obliqua and postprotocristid in the M_1 ; a well-developed anterobuccal ridge off the entoconid apex; and in lacking the hypoconid-entoconid crest on $M_{2.4}$.

Nimiokoala differs from *Perikoala* in being less crenulated; lacking the lingual shelf basal to the metaconid and entoconid on the lower molars; and in those features listed for *Madakoala*.

Nimiokoala differs from *Litokoala*,

Phascolarctos and *Cundokoala yorkensis* in: having a bulbous, less trenchant P^3 ; lacking the bulbous cuspid at the anterolingual base of the metaconule of M^1 (M^1 unknown for *L. kamunkaensis*) and the resultant pocket developed between the premetaconule crista, postprotocrista and the lingual margin; lacking the anterolingual protocone crest on M^1 ; lacking a metastylid fold; lacking buccal ribs on the protoconid, metaconid and entoconid; having a discontinuous lingual ectolophid wherein the postmetacristid and preentocristid do not meet; having a weaker entostylid; and in having less separation between the protoconid and paraconid on M_1 (M_1 unknown for *L. kutjampensis*).

Nimiokoala greystanesi differs from *L. kutjampensis* in lacking the buccal extension connecting the paracone to the buccal margin. *Nimiokoala* differs from *L. kamunkaensis* in: having a posterolingual cuspid on P_3 ; a greater separation of the anterior and posterior apices of P_3 and a more cusped anterior apex of that tooth; lacking the lingual and buccal ribs from the main apices on P_3 ; lacking an entoconid lingual shelf (postentostylid cristid) and metaconid lingual shelf; and in lacking a posterolingual protoconid ridge on M_4 .

Nimiokoala differs from *Phascolarctos* and *Cundokoala yorkensis* in: having a large posterolingual cusp on P^3 and strong anterior, buccal and lingual crests that extend from the anterior apex of that tooth; lacking the lingual cingular ridge of P^3 ; having proportionately wider upper molars; lacking the pocket at the anterior base of the protocone on M^1 ; having a proportionately less elongate P_3 ; having a large posterobuccal cusp on P_3 and strong anterior and buccal crests extending from the most anterior apex of that tooth; having a preprotostylid cristid on M_1 that is not continuous with the anterior cingulum; lacking the transverse connection between the apices of the metaconid and protoconid on M_2 ; lacking the columnar stylids of the metaconid and entoconid on $M_{1.4}$; and in lacking the lingual ridge connecting the bases of the protoconid and hypoconid on $M_{2.4}$.

REMARKS. *Nimiokoala* sp. is known only from a dentary fragment with $M_{2.4}$. Comparisons involving the upper teeth of this genus are therefore confined to features of *N. greystanesi* sp. nov.

ETYMOLOGY. Latin *nimio*, excessive; refers to the complex molar morphology relative to other phascolarctids.

Nimiokoala greystanesi sp. nov.
(Figs 1-3; Table 1)

ETYMOLOGY. For Greystanes High School, winner of the Sydney Morning Herald/ Riversleigh competition.

MATERIAL. Holotype QMF30482, cranial fragment with parts of the left and right maxillae, jugals and palatine, part of left premaxilla and part of right frontal. The left alveoli of I^{1-3} , P^3 , M^{1-3} and right P^3 , M^{1-2} , from Neville's Garden Site, System B (Archer et al., 1989), early to middle Miocene. Other material: Boid site east - QMF30483 partial skull with the left and right premaxillae, nasals, palatine, part of the left and right jugals, right frontal, part of right parietal, part of basisphenoid and basioccipital, part of right tympanic bulla, left I^{1-3} , C^1 , P^3 and anterior half of M^1 , right I^1 , alveoli of I^{2-3} , alveolus of C^1 , P^3 (missing buccal margin) and M^1 (which is missing the enamel from the parastylar corner); QMF30484, right M^{2-4} ; QMF30485, left M^2 ; QMF30486, left M^2 fragment with posterior part of metaconule and the neometaconule preserved; QMF30487, right dentary fragment with alveolus of I_1 , broken P_3 , M_1-4 ; Neville's Garden Site - QMF30512, right M^1 ; QMF23026, left M^2 ; QMF24232, left M^2 ; QMF24267, right M^2 ; QMF24233, left M^4 ; QMF20901, left M^4 and right M^4 ; QMF23027, left M^4 and right M^4 ; QMF29624, right dentary with P_3 , M_1-3 ; QMF30488, left M_1 ; QMF30489, right M_1 ; QMF24266, right M_1 ; QMF24265, right M_2 ; QMF20903, left M_2 ; Camel Spoutum Site - QMF30490, left P^3 ; QMF30491, left dentary with I_1 , alveolus of P_3 and alveolus of M_1-2 ; QMF30492, broken right M_3 ; QMF24351, right P_3 ; Inabeyance Site - QMF30493, left dentary fragment with I_1 , P_3 , M_1-2 , M_3 missing the anterobuccal corner, M_4 missing the buccal margin of the protoconid and the posterobuccal tooth corner. Dirk's Towers Site - QMF24516, molar fragment; QMF24291, left M^2 fragment; Rat Vomit Site - QMF30494, left dentary fragment with P_3 , M_1-3 (all missing the lingual margin), and alveolus of M_4 ; Upper Site - QMF30495, left P^3 ; QMF30496, right P^3 ; QMF30497, right M^3 ; RSO Site - QMF30498, left M^3 ; QMF30499, talonid of M_3 .

DIAGNOSIS. *N. greystanesi* differs from *Nimiokoala* sp. in having: less rounded lower molars; less lingually sloping surfaces of the metaconid and entoconid; a slightly larger entostylid ridge; a larger neomorphic cuspid in the trigonid basin in M_2-4 ; and a lesser reduction of the talonid in M_4 .

DESCRIPTION. Incisors. Left and right I^1 of QMF30483 short, pointed, with convergent tips, with enamel restricted to the anterior tooth face, with posterolingual faces dominated by large, triangular wear facets. Left I^2 small, subovate in

occlusal view, tapering anterolingually, without enamel on the occlusal surface. Left I^3 small, pointed, peg-like, contacting posterobuccal corner of the left I^2 , with enamel preserved on the buccal face.

Canines. Left canine short, peg-like, approximately 4mm behind the upper incisor arcade.

P^3 . LP^3 relatively robust, bulbous, wider posteriorly than anteriorly, with 5 majors cusps, 3 of which lie along a slightly crescentic longitudinal crest with an additional posterobuccal and posterolingual cusp. The anterior most cusp 1.61mm posterior to the anterior tooth margin. Prominent crests extending anteriorly, posteriorly and buccally from its apex; anterior crest bifurcating into anterior and posterolingual spurs; spurs extending towards the base of the crown. Medial cusp separated from the anterior cusp by a deep crevice, connected to the posterior cusp by a short longitudinal crest. Apex of the medial cusp 2.32mm posterior to the anterior tooth margin. Well-developed crest extending anterobuccally from the medial apex, fading into the base of the crown. Posterior cusp 3.19mm behind anterior tooth margin, with well-developed posterior crest extending from its apex: bifurcating at the base of the cusp, with one arm continuing posteriorly and fading into the base of the crown; other cingulum-like arm curving around the lingual tooth margin, connecting to the posterior crest of the well-developed posterolingual cusp. Posterolingual cusp apex opposite and slightly posterior to the medial cusp, with an anterolingual ridge fading into the lingual base of the crown from the apex. Posterobuccal cusp opposite, but slightly anterior to the posterior apex, with a well-developed crest extending posterobuccally from the apex, and fading into the base of the crown. An additional small cusplule at the anterior base of the posterolingual cusp.

RP^3 similar to LP^3 , but with less worn, medial cusp, smaller posterolingual cusp having weaker posterior crest extending from below the cusp apex and more distinct posterobuccal cusp.

Upper premolars (QMF30490, QMF30495, QMF30496) resemble P^3 of the holotype except for: buccal and lingual crests of the anterior cusp, the anterobuccal crest of the medial cusp and the posterobuccal crest of the posterobuccal cusp are reduced in QMF30495; undivided posterior crest of the posterior cusp fading into the anterior base of the crown in QMF30495, QMF30490 and QMF30496; small cusplule at the anterior base of the posterolingual cusp absent in QMF30495 and

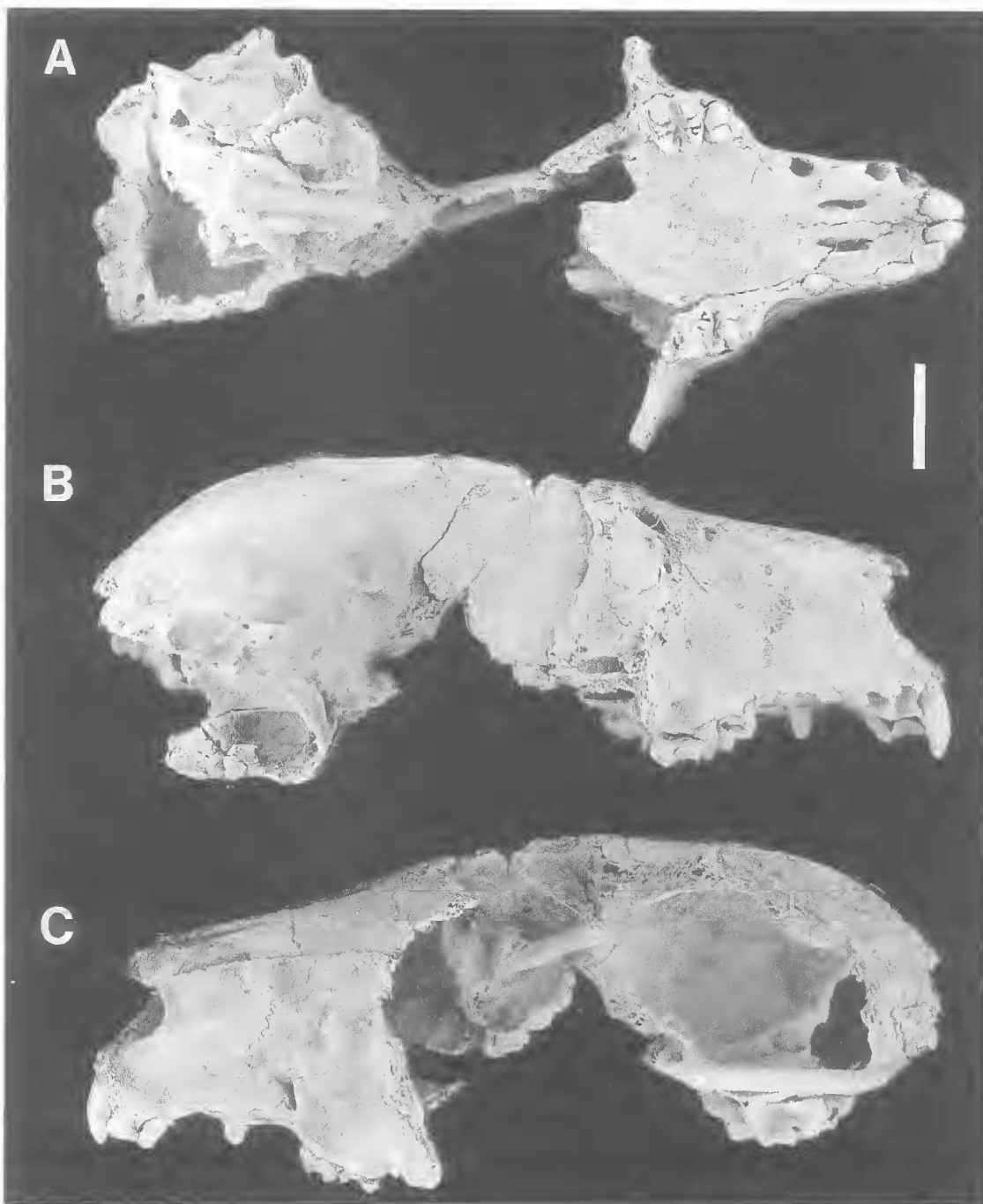


FIG. 1. Partial skull of *Nimiokoala greystanesi* gen. et sp. nov., QMF30483: A, ventral view; B, right lateral view; C, left lateral view. Bar = 10mm.

QMF30496; enamel missing from most of the occlusal surface of larger QMF30490 with re-

duced buccal crest of the anterior cusp, terminating before reaching the base of the crown.

M¹. Buccal margin of left M¹ slightly concave,

sloping anterolingually opposite the metacone; apices of the metacone and paracone slightly overhanging their lingual bases; lingual bases of paracone and metacone more lingually sloping in QMF30483 and QMF30512 than in the holotype; metacone taller than paracone; metaconule taller than protocone; parastylar corner, posterior and anterior base of metacone, posterior base of paracone, buccal bases of protocone and metaconule, lingual bases of paraconule and neometaconule and transverse valley crenulated. Paraconule well-developed, crescentic, cusped, occupying the longitudinal valley between paracone and protocone, bifurcate anteriorly; main arm extending anterobuccally and connecting to the anterolingual base of the parastylar corner, with two shorter, anteriorly directed spurs terminating at the base of the anterior cingulum and meeting the anterior cingulum in QMF30483. Posteriorly paraconule connecting to a strong posterolingual paracrista and a well-developed crest extending posterobuccally from the protocone apex; this connection more advanced in LM²⁻³. Paraconule not bifurcate posteriorly in RM¹ of holotype (or in QMF30483) but connecting to the posterolingual paracrista. Posteriorly bifurcate paraconule in QMF30512 without connection to the posterobuccal protocone crest. Large, crescentic, bicusped neometaconule occupying longitudinal valley between metacone and metaconule in M¹. Neometaconule in LM²⁻³ divided into two distinct cusped V-shaped structures. Neometaconule highly variable. In LM¹ of holotype connected to premetaconule crista by short anterior spur (not in RM¹), with second spur extending anterobuccally from the neometaconule and terminating in the transverse valley. In QMF30512 anterobuccal arm continuous with well-developed transverse ridges occupying the transverse valley of that tooth. Neometaconule connecting to anterolingual metacrista in RM¹ of QMF30483. Bifurcating posteriorly in LM¹ of the holotype: Short posterolingually directed spur meeting a well-developed crest extending posterobuccally from the metaconule apex (these structures not meeting in RM¹ of the holotype); main arm of the neometaconule extending posterobuccally, meeting both the posterolingual metacrista and the posterior cingulum. Neometaconule not meeting posterolingual metacrista or posterior cingulum in QMF30483 and QMF30512. Slightly crescentic preparacrista extending anterobuccally from the paracone apex to the buccal margin, bifurcating, with one arm continuing anterobuccally to

meet the postparastylar crista; second arm extending posterobuccally, connecting with stylar cusp B. Slightly longer postparacrista bifurcating at the buccal margin; with one arm continuing posterobuccally to meet the premetacrista at the buccal margin; with second arm extending anterobuccally to meet stylar cusp C at buccal tooth margin. Paracone buccal basin closed on M¹ of holotype, variably closed in other specimens. Metacone with stylar cusps D and E reduced (stronger on QMF30512); with buccal basin shallow and open. Height of the stylar cusps decreasing progressively from the parastyle to E. Strong posterolingual paracristae, anterolingual metacristae and posterolingual metacrista in the upper molars of the holotype. Anterolingual paracristae in QMF30512, QMF20901 and QMF23027. Protocone apex opposite but slightly posterior to the paracone apex, slightly lingual relative to the metaconule apex. Crescentic postprotocrista and premetaconule crista meeting in the transverse valley well buccal to the lingual tooth margin. A series of short spurs extending buccally from this junction, terminate in the transverse median valley. Protostyle well-developed, at the anterobuccal base of the protocone, extending posteriorly from the preprotocrista, terminating at the buccal base of the protocone opposite the apex of the paraconule. Surface enamel crenulations in the transverse valley of the LM¹ aligned into two parallel (discontinuous) transverse crests, contrasting with the reticulate pattern in RM¹ and more posterior molars of holotype. Distinct transverse crests occupying the transverse valley in QMF30483 and QMF30498.

M²⁻³. Similar in most aspects to LM¹ except for: teeth tapering more posteriorly, triangular buccal surfaces of the paracone and metacone sloping more steeply to the buccal margin; buccal margin more concave, buccal margin of the metacone sloping more posterolingually; parastyle absent; more reticulate crenulations; reduced stylar cusps; a deep pocket formed by the junction of the premetaconule crista, postprotocrista, the posterobuccal crest of the protocone and the posterolingual arm of the paraconule; protostyle reduced, connecting to the paraconule; neometaconule reduced, divided into 2 distinct V-shaped structures; neometaconule meeting anterolingual metacrista; a vague anterolingual paracrista in LM²⁻³.

M⁴ (Fig. 2B). Paracone, paraconule and protocone at similar stage of development to M³ of the holotype. Metacone and metaconule ex-

tremely reduced to small cusps on the posterobuccal and posterolingual margins, respectively. Posterior margin crescentic, consisting of a series of ridges extending anteriorly into the transverse valley. Premetacrista forming part of the posterior margin, curving anterobuccally around the tooth margin to meet the postparacrista at the buccal exit of the transverse valley. Neometaconule reduced, indistinguishable from the enamel crenulations.

Right dentition of the holotype similar to the left except for: smaller RM¹; less convex buccal margin; paracone and metacone sloping more gently to the buccal margin; deeper and less crenulated transverse valley lacking parallel transverse ridges; protocone higher than the metaconule; paraconule and neometaconule taller and less crescentic; paraconule apex closer to the protocone, not bifurcate anteriorly, without connection to the posterobuccal crest of the protocone; neometaconule not bifurcate anteriorly; protostyle weaker; anterolingual paracrista vaguely developed in the right M¹.

LOWER DENTITION (Figs 2C, 3A-C). I₁. Incisor narrow, lanceolate, with enamel covering ventral and buccal surfaces of the anterior half, with fine shallow longitudinal groove linearly along the buccal margin terminating approximately 1 mm posterior to anterior tip of tooth.

P₃. LP₃ small, short longitudinally, of 3 aligned main cusps (anterior, medial and posterior), a large posterobuccal cusp and a small posterolingual cusp; lingual surface sloping steeply to the lingual tooth margin; shallow crevice separating the anterior cusp from the medial cusp; medial apex connected to the posterior cusp by a short longitudinal crest; prominent anterolingually directed crest and posterobuccally directed crest extending from the anterior apex and fading into the base of the crown; prominent crest connecting posterior cusp to posterior cingulum; apex of the posterobuccal cusp opposite and slightly posterior to the posterior cusp. Short anterobuccally and posterolingually directed crests extending from the apex of the posterobuccal cusp.

Lower molars distorted, with metaconid and entoconid anteriorly displaced relative to the protoconid and hypoconid, respectively.

M₁. Subrectangular, anteriorly attenuated; hypoconid largest cusp on the talonid; protoconid largest cusp on the trigonid; well-developed protostylid at the buccal margin, opposite and slightly posterior to the protoconid apex. Pro-

tostylid and hypoconid pyramidal in occlusal outline in QMF30493 but more rounded in QMF30494. Preprotocristid extending anterolingually from the protoconid apex to a relatively small paraconid at the anterolingual corner (in QMF30488 paraconid connected to the premetacristid by a short longitudinal crest). Premetacristid poorly developed. Linear postprotocristid extending posteriorly into the central basin, meeting the crenulated cristid obliqua slightly lingual to the longitudinal tooth axis; postmetacristid extending posterolingually towards the weakly developed metastylid at the lingual tooth margin, with a well-developed posterolingually directed ridge branching off and extending into the transverse valley separating the talonid and trigonid. Crescentic preprotostylid cristid curving anterolingually along the anterior tooth margin, connecting to the anterobuccal base of the protoconid, this connection slightly more lingual in QMF30488 and slightly more buccal in QMF30489. Postprotostylid cristid extending towards the lingual margin, terminating at the anterior base of the hypoconid; less developed in QMF30488 and QMF30494, fading into the posterior base of the protostylid. Well-developed posterolingually developed crest extending from the protostylid apex, terminating at the posterior end of the longitudinal crevice separating the protostylid and protoconid, more crescentic and with an additional short lingual ridge extending from the protostylid apex in QMF30488. Preentocristid extending anterobuccally (as opposed to anterolingually in other phascolarctids) into the transverse valley separating talonid from trigonid. A second crest extending anterobuccally from the entoconid apex, running parallel to the preentocristid. An additional buccally directed crest extending from the entoconid apex into the valley separating the bases of the entoconid and entostylid ridge. Postentocristid extending posteriorly along the lingual margin to a poorly developed entostylid at the posterolingual corner of the tooth. Large cusped ridge in the longitudinal valley between the entoconid and hypoconid analogous to, although more strongly developed than, the entostylid ridge in *Litokoala* and *Phascolarctos*. Entostylid ridge bifurcating anteriorly; two anterobuccally directed ridges extending from its apex, meeting the cristid obliqua. Bifurcating posteriorly; two posterolingually directed ridges terminating at the base of the posterior cingulum. Entostylid not bifurcate in QMF30494.

M₂₋₃. M₂ and M₃ similar to M₁ except for:

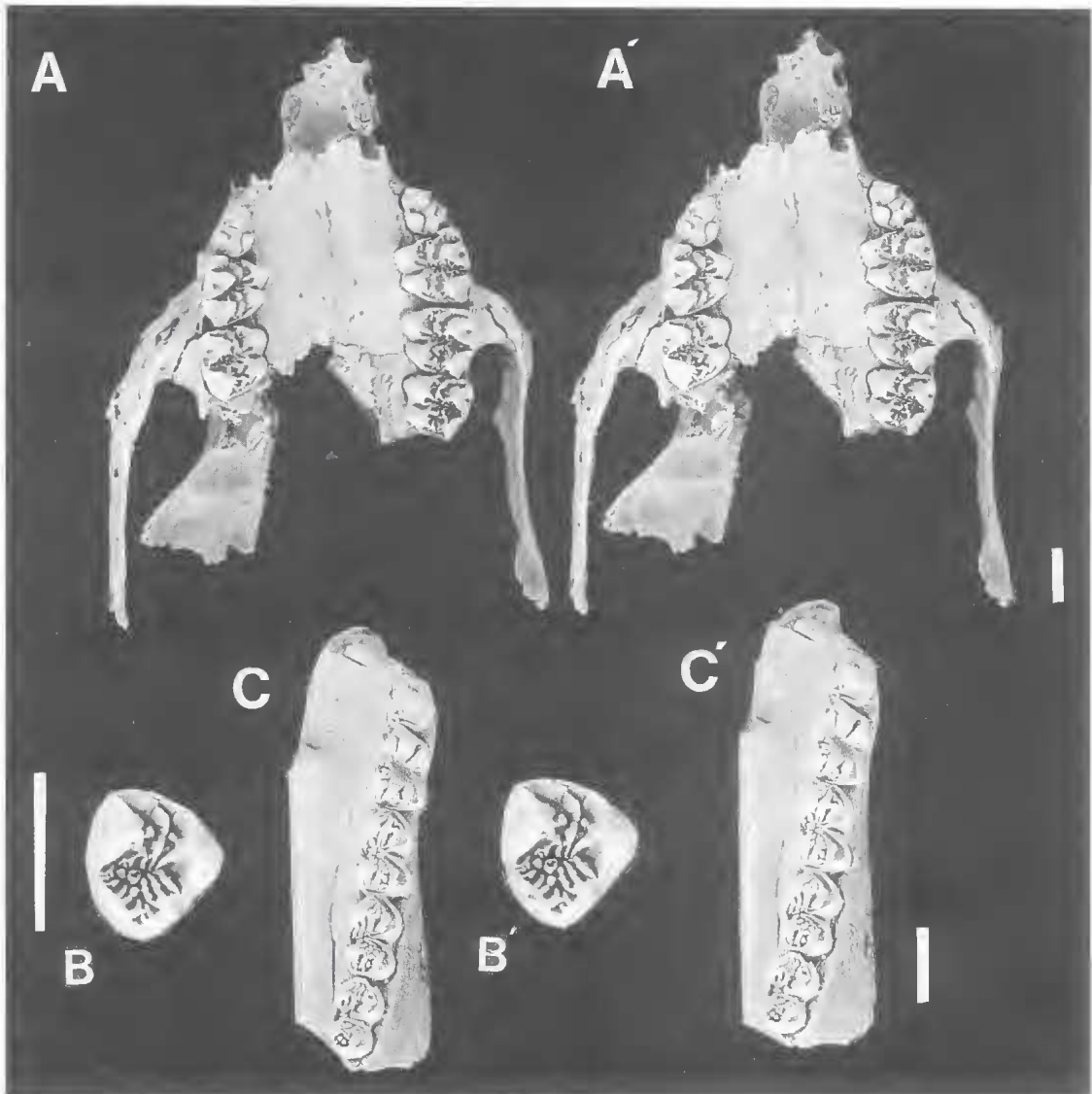


FIG. 2. *Nimiokoala greystanesi* gen. et sp. nov. A-A', QMF30482, holotype, occlusal stereopair of rostral region. B-B', QMF23027, right M⁴, occlusal stereopair. C-C', QMF30487, right dentary fragment, occlusal stereopair. Bar = 5mm.

protostylid absent; paraconid absent; preprotocristid continuous with anterior cingulum; postprotocristid linear, extending posterolingually towards its junction with the cristid obliqua; premetacristid more prominent, continuous with the anterior cingulum; entostylid reduced resulting in a more rounded posterolingual tooth corner; entostylid ridge reduced, not bifurcate; entoconid reduced in M₃; hypoconid reduced; preentocristid and posterobuccal metacristid joining, closing the transverse valley well buccal

to the lingual tooth margin. A neomorphic cuspid in the longitudinal valley between the metaconid and protoconid in M₂₋₄, with a well-developed posterolingually directed ridge and a weaker anterobuccally directed ridge extending from its apex, more strongly developed and more separated from the metaconid in M₂₋₄ of QMF30487 than of QMF30493.

M₄. M₄ similar to M₂₋₃ except for; entostylid ridge further reduced, connecting posteriorly to the posterior cingulum; neomorphic cuspid re-

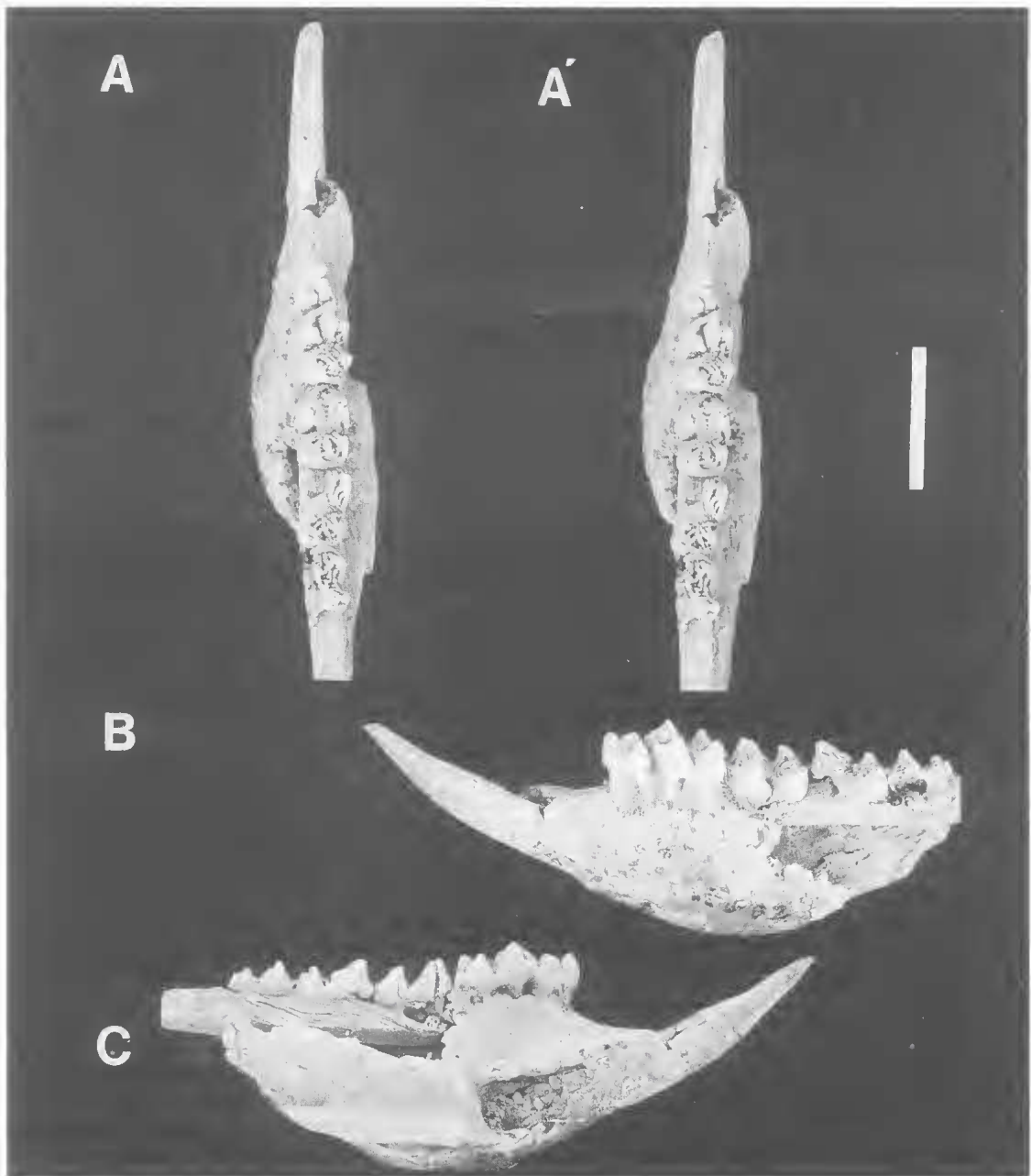


FIG. 3. *Nimiokoala greystanesi* gen. et sp. nov. A-C, QMF30493. A-A', occlusal stereopair of left dentary. B, buccal view. C, lingual view. Bar = 10mm.

duced; postprotocristid and cristid obliqua not meeting end to end but parallel each other (as in *L. kanunkaensis* and some *P. cinereus*); talonid severely reduced resulting in a greater anterior displacement of the entoconid and metaconid

(relative to the hypoconid and protoconid, respectively) (as in *L. kanunkaensis* and some pseudocheirids).

REMARKS. QMF30482 (Fig. 2A) was chosen as

TABLE 1. Dentition measurements (mm) for *Nimiokoala greystanesi* sp. nov. and *Nimiokoala* sp. (last line SAMP19952 only). L=length; W=width; AW, anterior width; PW, posterior width; *=estimate.

A. UPPER CHEEK DENTITION															
Spec.	Side	P3		M1			M2			M3			M4		
		L	W	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW
QMF30482 Holotype	L	4.50	3.98	6.45	5.94	5.66	6.05	6.18	5.52	5.70	5.67	4.63			
	R	4.48	3.51	5.99	5.74	5.35	5.92	5.90	5.54						
QMF30483	L	4.51	3.95	L	5.39	-									
	R	4.63	3.83	6.30	5.47	5.68									
QMF30484	R						5.53*	5.63	5.22	5.16	5.15	4.46	4.60	4.48	2.12
QMF30490	L	4.87	4.15												
QMF30495	L	4.52	3.68												
QMF30496	L	4.46	3.53												
QMF30512	L			6.01	5.99	5.93									
QMF24267	R						6.12	6.14	5.41						
QMF24232	L						6.18	6.01	5.42						
QMF30485	L						-	-	5.23						
QMF30498	L						5.18	5.27	4.85						
QMF23026	R						5.67	5.88	5.52						
QMF30497	R									5.28	5.28	4.72			
QMF24233	L												4.12*	3.96	1.91
QMF23027	L												4.47	4.24	2.65
	R												4.67	4.32	2.62
QMF20901	L												4.68	4.69	2.81
	R												4.29	4.16	2.30
B. LOWER CHEEK DENTITION															
QMF30487	R	4.10	3.00	5.70	3.15	3.69	5.77	3.28	3.62	5.56	3.19	3.28	5.07	3.16	3.00
QMF30493	L	3.35	2.44	5.95	3.54	3.40	5.85	3.40	3.43	5.50	-	3.04	5.10	-	-
QMF30494	L	3.63	2.46	5.37	L	3.41	5.86	3.22	3.28	5.57	3.17	3.05			
QMF29624	L	3.86	2.54	5.91	3.07	3.48	5.75	3.26	3.34	5.53	3.30	3.12			
QMF24351	R	3.21	2.25												
QMF24266	R			6.22	4.29	3.66									
QMF30488	R			6.19	3.42	3.65									
QMF30489	R			5.96	3.45	4.04									
QMF20903	L						6.31	3.55	3.92						
QMF24265	R						5.84	3.27	3.30						
SAMP19952	L						5.04	2.77	3.00	5.18	2.95	2.88	4.32	2.53	2.19

holotype because it contains most of the upper dentition well-preserved and relatively unworn. The holotype is thought to represent a juvenile because of the shorter premaxilla in comparison with the adult skull, QMF30483.

Nimiokoala sp.
(Fig. 4, Table 1)

MATERIAL. SAMP19952 left dentary with alveoli of P3 and M1, M2-4 intact from late Oligocene to middle

Miocene South Prospect B locality, Lake Namba, Frome Downs Station, South Australia.

REMARKS. Enamel is missing from the lingual margins of the metaconids and entoconids and the buccal margins of the protoconids and hypoconids. Features of the M2 are difficult to discern because of extreme wear in that tooth. Only points of difference from *N. greystanesi* are noted here.

Lower molars are proportionately smaller (by approximately 15%) and more rounded, espe-

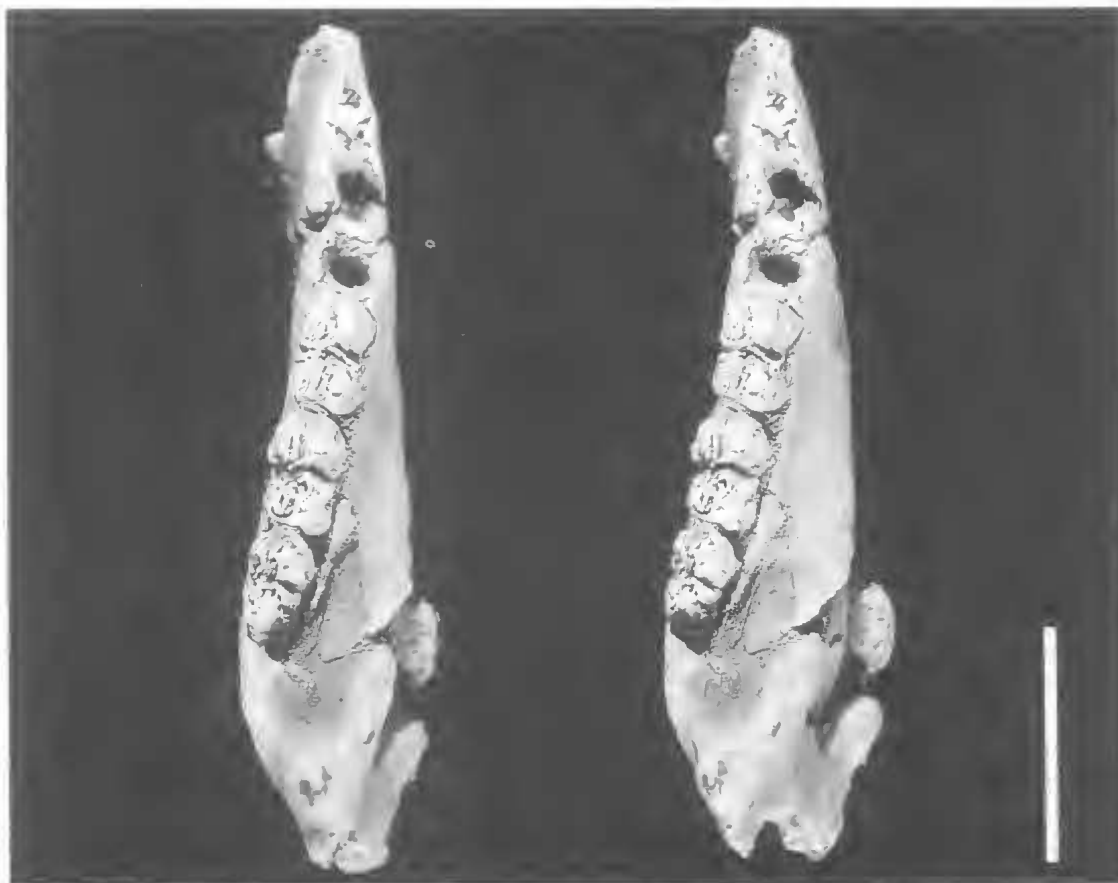


FIG. 4. *Nimiokoala* sp., SAMP19952, from South Prospect B Locality, Lake Namba, South Australia. Occlusal stereopair of right dentary. Bar = 10mm.

cially the talonid. The neomorphic cuspid between the metaconid and protoconid in M_{2-4} is weaker, as is the entostylid ridge. The lingual surfaces of the protoconid and metaconid slope more lingually. The talonid of M_4 is further reduced.

This taxon is left in open nomenclature in the absence of the upper dentition. The features mentioned above as differences between the central Australian and Riversleigh materials vary significantly between individuals of *N. greystanesi* and may not be reliable species indicators.

Litokoala Stirton, 1967

TYPE SPECIES. *Litokoala kutjampensis* Stirton, 1967.

OTHER SPECIES. *Litokoala kanunkaensis* Springer, 1987.

DIAGNOSIS. *Litokoala* differs from other phascolarctids in having a posterobuccal crest extending from the apex of the metaconid on M_{2-4} (although this crest is reduced on M_4); a well-developed posterolingually directed crest from the protoconid apex of M_4 . *Litokoala* differs from other phascolarctids except *Phascolarctos* and *Cundokoala yorkensis* in: having a neomorphic cuspule at the anterior base of the metaconule of M^1 ; an anterolingual protocone crest on M^1 and consequently a much squarer anterolingual margin of that tooth; a metastylid fold wherein the postmetastylid cristid is continuous with the preentocristid; an anteriorly bifurcate preentocristid on the lower molars; and internal ribs on the metaconid and hypoconid of M_1 .

Litokoala differs from all other phascolarctids except *Nimiokoala* in having: a well-developed crescentic paraconule and neometaconule on upper molars; an anteriorly displaced entoconid

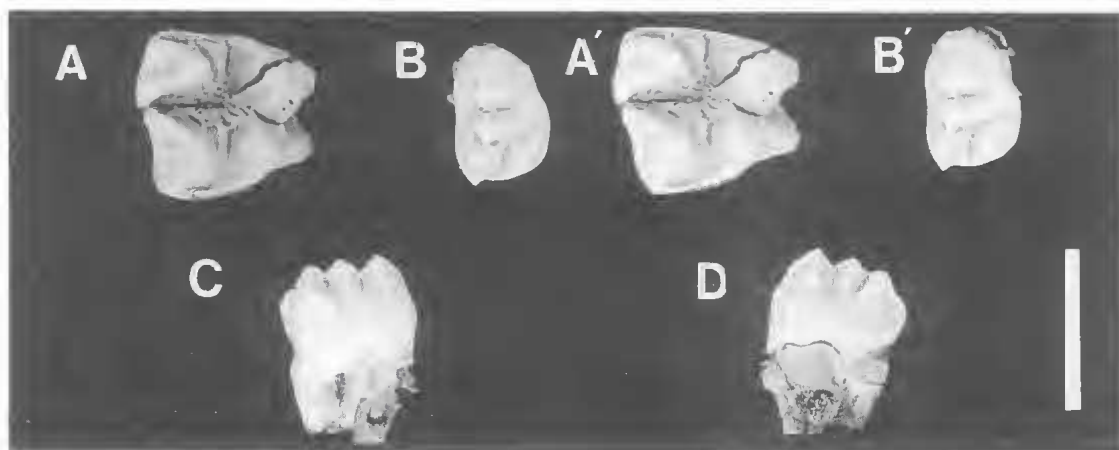


FIG. 5. *Litokoala kanunkaensis*, Henk's Hollow Site, Riversleigh Station. A-A', QMF30502, RM³ occlusal stereopair. B-D, QMF30500, RP₃. B-B', occlusal stereopair. C, buccal view, D, lingual view. Bar = 5mm.

(relative to the hypoconid) on M₄; an anteriorly displaced metaconid (relative to the protoconid) on M₄; and a parallel arrangement of the postprotocristid and cristid obliqua on M₄ wherein these cristids do not meet end to end.

Litokoala differs from *Koobor* in: being smaller; having less rounded bases of the paracone, metacone, protocone and metaconule; having less elongate molar proportions; reduced styler cusps; a paraconule on M³; and a neometaconule on M¹⁻³.

Litokoala differs from *Madakoala* and *Perikoala* in: being smaller; higher crowned; more selenodont; having a larger neometaconule; a more crescentic, less linear paraconule; an entostylid ridge in the lower molars; a more lingual junction of the cristid obliqua and postprotocristid; a larger developed protostylid and a more lingual protoconid on M₁; a less strongly developed, more buccally positioned paraconid on M₁; and a more strongly developed entostylid.

Litokoala differs from *Perikoala* in: lacking the well-developed styler border of the paracone and metacone; lacking the additional styler cusp anterior to styler cusp E; having a weaker entoconid lingual shelf; and a weaker premetacristid.

Litokoala kutjamarpensis differs from *Madakoala* and *Perikoala* in having a buccal extension of the paraconule which connects to the buccal margin of M¹. *Litokoala kanunkaensis* differs from *Madakoala* and *Perikoala* in: lacking the M₂ protostylid ridge; having a less elongate P₃; a more prominent posterobuccal cusp;

and having 3 apices on the longitudinal crest (4 in *Madakoala devisi*; 5 in *M. wellsii*) on P₃.

Litokoala differs from *Nimiokoala* in: having less steeply (more buccally) sloping buccal surfaces of the paracone and metacone; lacking the division of the neometaconule in the more posterior molars; lacking the well-developed posterobuccal crest from the apex of the metaconule; having a weaker posterobuccal crest from the protocone apex; lacking the posterolingual ridge off the apex of the protostylid on M₁; having a less cusped, more posteriorly positioned entostylid ridge; having an anterolingually (as opposed to anterobuccally) directed preentocristid; a more posterolingually directed postprotostylid cristid; a lingual entoconid shelf; and a more strongly developed entostylid. *Litokoala kanunkaensis* differs from species of *Nimiokoala* in: lacking the posterolingual cusp on P₃; in having a weaker anterior cusp on P₃; buccal and lingual ribs which extend from the main apices of the longitudinal crest in the P₃; and in lacking the neomorphic cuspid between the metaconid and protoconid of M₂₋₄.

Litokoala differs from *Phascolarctos* and *Cundokoala yorkensis* in: being smaller; having well-developed anterolingual metacristae; having proportionately less elongate lower molars; a less pronounced entoconid basal shelf; and in lacking the ridge connecting the buccal bases of the protoconid and hypoconid of M₂₋₄.

***Litokoala kanunkaensis* Springer, 1987**
(Figs 5-6, Table 2)

MATERIAL. Holotype SAMP32397 (=UCR21926) a right M₂ from latest Oligocene UCR Locality RV-8453 Kanunka North Local Fauna, Etadunna Formation, west side of Lake Kanunka, South Australia. Other material: from Kanunka North Site: UCR21945, a right M₄; UCR21980, a metacone of a right M₃; UCR21979, a metacone of LM¹; late Oligocene. From Henk's Hollow Local Fauna: QMF30500, right P₃; QMF13079, right dentary fragment with posterior half of P₃, M₁₋₂; QMF30502, right M₃; from Gag Site: QMF30501, right M₁; from Gotham Site: QMF30503, M⁸ fragment containing paracone and buccal half of protocone. From JC9 Site: QMF20809, right M₃; System C, Riversleigh, middle Miocene (Archer et al., 1989; 1991).

DIAGNOSIS. *Litokoala kanunkaensis* differs from *L. kutjamarpens* in: having a short longitudinal spur connecting the paracone to the anterior cingulum; lacking the bulbous cuspule at the anterolingual base of the metacone; lacking the protostyle (the latter two features may be result of differences along the tooth row rather than interspecific differences); lacking the distinct posterolingual and anterolingual paracrista; having a strong anterobuccal crest from the metacone apex.

COMPARISON WITH THE HOLOTYPE. Prior to this study *L. kanunkaensis* was known from two isolated lower molars, an M₂ and M₄. Referral of the Riversleigh material to *L. kanunkaensis* is based on the similarity of the M₂ of QMF13079 to the holotype. Some small differences are: M₂ of QMF13079 is slightly larger; posterobuccal metacone strut is poorly defined and bifurcates in the trigonid longitudinal valley, one spur fading

ing buccally into the protocone base and the other spur continuing posteriorly then turning sharply lingually before becoming part of the molar crenulation pattern; the entostylid ridge is less cusped and arises from the posterobuccal base of the entocone (unlike the holotype in which it arises from the postentocristid); and the transverse median valley, the posterior base of the protocone, the cristid obliqua and the transverse valley separating the bases of the protocone and hypocone are more crenulated than in the holotype.

QMF13079 M₂ is significantly more worn than the holotype which may account for the poorer crest definition. Analysis of intraspecific variation in *Phascolarctos cinereus* and *Nimiokoala greystanesi* indicate that these differences do not warrant specific distinction. Most variable features in the modern species include: molar size; pattern and degree of molar crenulations; cristid obliqua; entostylid ridge. Although the entostylid ridge may be phylogenetically significant in phascolarctids, it is highly variable. It may be a well-developed cusped structure, relatively indistinguishable as a series of discontinuous crenulate ridges, completely isolated at the base of the entocone or variably connected to the postentocristid, the base of the entocone or the posterior cingulum. Hence differences between the holotype and QMF13079 are within intraspecific variation.

DESCRIPTION. P₃ (Fig. 5B-D). Short, semi-rectangular, of 4 major cusps anteriorly, medially, posteriorly and posterobuccally on the crown. Anterior, medial and posterior cusps on a longitudinal crest extending the length of the crown. Anterior cusp tallest, 1/3 of way along longitudinal crest, above the anterior root of P₃. Anterior, buccal and lingual crests extending from its apex; anterior crest fading into the anterolingual base of the crown; lingual crest fading down the lingual tooth margin, curving posterolingually at its tip; buccal crest short, fading into the buccal tooth margin. Anterobuccal, anterolingual and posterolingual crests extending from the posterior cusp apex; anterobuccal crest poorly developed, extending into the valley between the posterior and posterobuccal cusps, meeting a short lingual ridge from the posterobuccal cusp apex; anterolingual crest better developed, fading down the lingual margin; posterolingual crest curving anterolingually along the base of the crown, becoming cingulum-like, fading into the base of the posterior cusp. Posterobuccal cusp

TABLE 2. Measurements (mm) for right lower dentition of *Litokoala kanunkaensis* from Riversleigh's System C deposits. Abbreviations as for Table 1.

QMF No.	P ₃		M ₁			M ₂			M ₃		
	L	W	L	AW	PW	L	AW	PW	L	AW	PW
30500	4.12	3.10									
30501			4.72	2.63	3.04						
13079		2.62	4.89	3.14	3.58	5.15	3.43	3.57			
20809									5.48	3.39	3.40

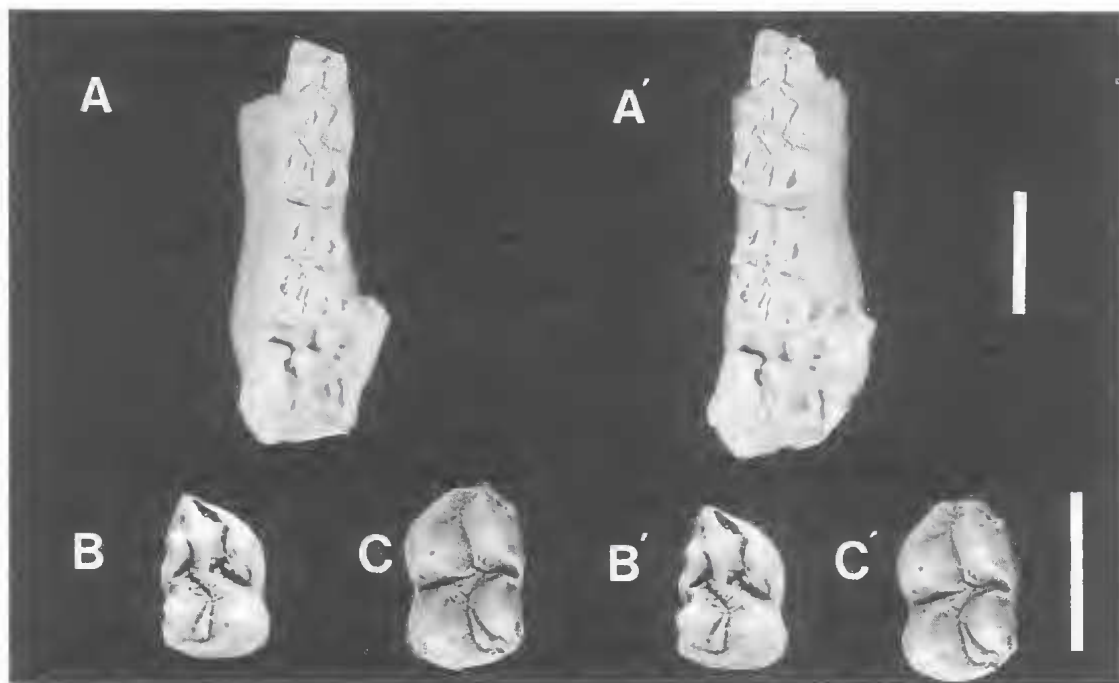


FIG. 6. *Liokoala kanunkaensis*. A-A', QMF13079, right dentary fragment with posterior half of P₃, M₁₋₂, occlusal stereopair. B-B', QMF30501, RM₁, occlusal stereopair. C-C', QMF20809, LM₃ occlusal stereopair. Bar = 5mm.

opposite but slightly posterior to the posterior cusp, with a short posterolingual ridge extending from its apex and terminating at the posterior end of the valley between the posterior and posterobuccal cusps, with short, anterobuccal crest extending from its apex and fading towards the base of the crown.

M₁ (Fig. 6B). Semi-rectangular, tapering slightly anteriorly. Protoconid most worn of the major cusps, with well-developed protostylid opposite but slightly posterior to apex. Short, linear cristid extending posteriorly from the apex of the protostylid into the transverse valley, bifurcating into posterolingual and posterobuccal arms, both arms terminating in the transverse valley between the talonid and trigonid. (In QMF13079 postprotostylid cristid more crenulated, bifurcation less distinct and more a part of the crenulation pattern). Anterolingual cristid from protostylid apex crescentic, well defined, continuous with the anterior eingulum extending to the anterolingual corner of the tooth. Lingual rib from the protostylid apex short, fading into its base. Crescentic, eingulum-like ridge extending posterobuccally from the posterobuccal base of the protostylid, fading into the anterior base of the

hypoconid. Preprotocristid extending anterolingually to the paraconid, a moderately developed, slightly cusped structure at the anterolingual tooth corner, with a posterolingually directed ridge fading down the lingual margin towards the base of the crown. Anterobuccal crest continuous with the anterior eingulum/preprotostylid cristid. Postprotocristid extending posteriorly meeting cristid obliqua slightly lingual to the longitudinal axis of the tooth. Postmetacristid extending posterolingually from the apex of the metaconid to the lingual margin, swelling at this point to form the metastylid. Posterolingual ridge from the metastylid short, fading down the lingual tooth margin, better developed in QMF13079. Postmetastylid cristid a short, buccal ridge, continuous with the preentocristid, resulting in the metastylid fold. Entoconid sub-pyramidal. Preentocristid extending anteriorly towards the transverse axis, curving lingually, bifurcating with one spur extending lingually to meet the postmetastylid cristid and other extending anterobuccally into the transverse valley to lingual base of the junction of the postprotoeristid and cristid obliqua. QMF13079 (Fig. 6A-A') with a short anterolingual spur ex-

tending from the junction of the postprotoeristid and cristid obliqua to the anterobuccal spur of the preentocristid. A well-developed anterobuccal ridge extending from the entoconid apex, terminating at the anterobuccal base of the entoconid, just lingual to the anterior arm of the entostylid ridge. Postentocristid curving posterolingually from the entoconid apex to the posterolingual tooth corner, swelling at this point to form a small entostylid. A short anterolingual ridge fading down the lingual tooth margin from the entostylid apex, better developed in QMF13079. A short posterobuccal ridge extending from the entostylid apex, continuous with the posterior cingulum. Well-developed cusped entostylid ridge at the posterobuccal base of the protoconid, fading anteriorly along the longitudinal tooth axis, with a shorter posterior spur terminating before meeting the posterior cingulum. QMF13079 with entostylid ridge extending buccally from the postentocristid, similar in this respect to the holotype. Hypoconid largest of the main cusps. Posthypoeristid extending posterolingually along the posterior tooth margin, becoming continuous with the posterior cingulum. Cristid obliqua long, well-developed, crenulated, relatively linear, extending anterolingually from the hypoconid apex, meeting the postprotoeristid on the transverse valley slightly lingual to the longitudinal axis. Talonid basin, transverse valley between the talonid and trigonid and buccal base of the entoconid and protoconid crenulated. Lingual base of the hypoconid and protostylid lightly crenulated. Protostylid occupying the anterobuccal corner of the tooth, lying well buccal to the longitudinal axis. Short lingual ribs extending from apices of the entoconid, hypoconid, protoconid and protostylid. Short buccal ribs off the protoconid and metaconid apices, less prominent in the holotype.

M₁ (Fig. 6C-C') is similar to the holotype except for: being slightly larger, having buccal bases of the protoconid and hypoconid more rounded, the lingual shelf of the metaconid better developed, the cristid obliqua and postprotoeristid meeting at a more lingual position, the anterobuccal entoconid ridge and the posterobuccal metaconid ridge poorly developed (possibly due to wear) and the entostylid ridge extending buccally from the postentostylid cristid rather than from the postentocristid.

M¹ (Fig. 5A-A') Length 5.16mm; anterior width 5.22mm; posterior width 4.28mm. Sub-quadrate, tapering slightly posteriorly, with shallow surface enamel crenulations in the transverse

valley and posterior base of paracone. Buccal bases of the protocone and metacone large, rounded, with lingual bases of all major cusps sloping gently lingually. Triangular buccal surface of paracone reduced relative to the metacone (less marked in QMF30503). Buccal margin of the paracone sloping anterolingually; buccal margin of the metacone sloping slightly posterolingually in occlusal view. Buccal basins of the paracone and metacone shallow and open. Buccal basin of the paracone deeper than that of the metacone. Styral cusps B and C well-developed on the paracone. Styral cusps on the metacone poorly developed, styral decrease progressively from B to E. In QMF30503 styral cusp C more strongly developed, almost closing the paracone buccal basin. Preparaerista relatively short crest, extending anterobuccally to the anterobuccal tooth corner, bifurcating, with one arm curving buccally and becoming continuous with the anterior cingulum, the other short ridge extending posterobuccally, fading along the paracone buccal margin to a slight swelling representing styral cusp B. Longer, relatively linear postparaerista extending posterobuccally to the buccal margin, meeting premetaerista, closing the buccal exit of the transverse valley. Styral cusp D a slight swelling at the buccal tip of the premetaerista. Postmetaerista linear, extending posterobuccally from the metacone apex to the posterobuccal tooth corner, meeting the posterior cingulum. Paraconule at the anterolingual base of the paracone, slightly cusped at this point, bifurcating anteriorly, with main linear arm extending anterobuccally, terminating at the anterolingual base of the paracone before meeting the anterior cingulum, with a minor arm connecting the anterior cingulum. Linear posterior arm of the paraconule extending posteriorly along the longitudinal valley between the paracone and protocone, bifurcating at a point just anterior to the transverse median valley. A short posterobuccal arm meeting the posterolingual paraerista; second arm continuing posteriorly into the transverse median valley. A cusped, anteriorly bifurcate neometaconule at the anterolingual base of the metacone, with the main crenulated arm extending anterobuccally, meeting the anterolingual metaerista at the base of the metacone. A shorter arm fading lingually from the neometaconule apex into the longitudinal valley at the buccal base of the hypocone. Posteriorly, the linear arm of the neometaconule fading into the longitudinal valley between the metacone and metaconule. Buccal surfaces of the protocone and

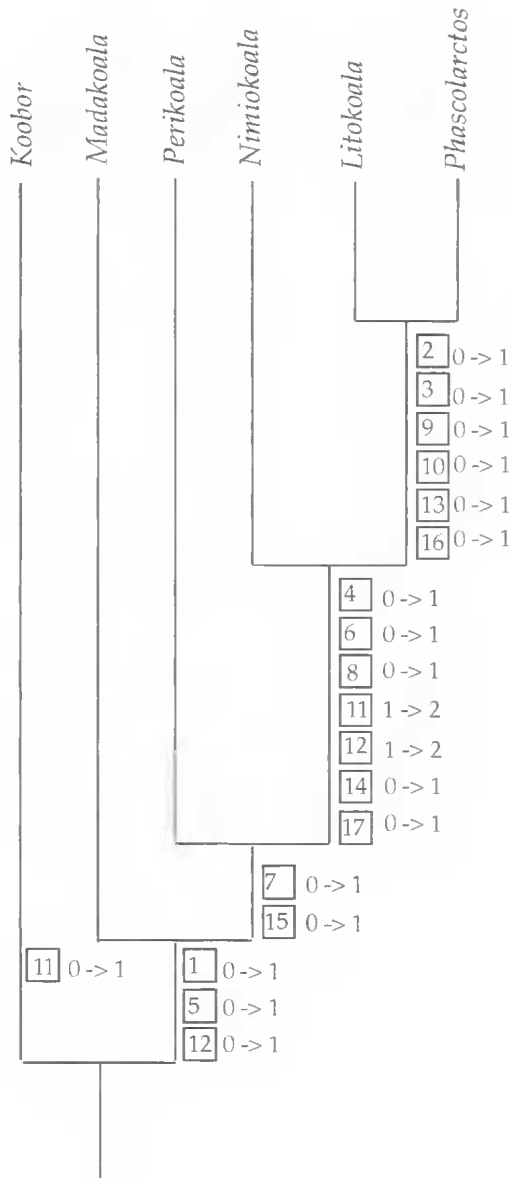


FIG. 7. Phylogeny of the Phascolarctidae based on cladistic analysis of dental characters (Table 3). Apomorphies are represented by boxed numbers. Arrows indicate character state transformations. 0 = plesiomorphic character state; 1 = derived character state; 2 = most derived character state.

metaconule sloping gently buccally. Preprotocrista long, crescentic crest, extending anterobuccally, curving more buccally into the longitudinal valley, meeting the anterior spur off the paraconule, becoming continuous with the

anterior cingulum. The slightly more crescentic postprotocrista extending posterobuccally toward the transverse valley, turning sharply buccally, meeting the short, slightly crescentic prehypocrista at the buccal end of the transverse valley between the metaconule and protoconule. Prehypocrista bifurcating just posterior to the transverse valley, with one arm continuing anterobuccally to the postprotocrista, with the other crenulated arm extending buccally, then anterobuccally into the transverse median valley. Junction of the postprotocrista and prehypocrista effectively sealing off the lingual exit of the transverse valley well-in from the lingual margin. Two short ridges at the posterolingual base of the protoconule and the anterolingual base of the metaconule. Posterolingual base of the protoconule slightly crenulated and cingulum-like. The long, slightly crescentic posthypocrista extending posterobuccally, becoming continuous with the posterior cingulum. A relatively well-developed anterobuccal ridge from the metaconule apex, fading towards its base. Posterobuccally directed ridge from the protoconule apex fading into the posterobuccal base of the protoconule. Posterolingual paracrista bifurcating at its base, one arm meeting the anterobuccal arm of the paraconule and continuing into the transverse median valley, with the other extending posterobuccally into the transverse median valley. Anterolingual metacrista bifurcating at the anterolingual base of the metaconule, one arm continuing anterolingually to meet the anterobuccal arm of the neometaconule, the other extending anterobuccally into the transverse valley between the paraconule and metaconule.

PHYLOGENETIC ANALYSIS

Seventeen dental characters which provide phylogenetically useful data on phascolarctid relationships are analysed (Tables 3, 4). Character polarities were determined using selenodont ilariids and subselenodont wynyardiids as outgroups.

CHARACTER ANALYSIS

Thirty potentially useful dental characters were reduced to 17 following analysis of variation in the living species. The Pleistocene *Cundokoala yorkensis* Pledge, 1992 is not significantly different in dental morphology from *Phascolarctos*; generic distinction is not warranted. It is here regarded as a separate species of *Phascolarctos*.

TABLE 3. A list of character state polarities (PLES= plesiomorphic state; APO= apomorphic state) for the Phascolarctidae using ilariids and wynyardiids (Marsupialia: Vombatiformia) as outgroups. A=absent; P=present; LI=linear; C=crescentic; LA=large; R=reduced; W=weak; S=small; M=moderate; B=buccal; LIN=lingual third of trigonid

CHARACTER	PLES	APO
1. Bladed premolar	A	P
2. Trenchant premolar	A	P
3. Posterobuccal cusp on P ³	P	A
4. Structure of paraconule	LI	C
5. Development of neometaconule	A	P
6. Protostyle development	A	P
7. Styler cusp development	LA	R
8. Posterolingual paracristae	A/W	P
9. Neomorphic cuspule at base of metaconule	A	P
10. Anterolingual protocone crest	A	P
11. Parastyle development on M ¹	S	M/L
12. Protostylid development on M ₁	A	P
13. Metastylid fold	A	P
14. Entostylid ridge	A	P
15. Position of protoconid on M ₁	B	LIN
16. Buccal ribs on lower molars	A	P
17. Anteriorly displaced entoconid relative to hypoconid and anteriorly displaced metaconid relative to protoconid in M ₄	A	P

1. *Premolar cusp pattern*: P³ in most phascolarctids (e.g. *Madakoala*, *Perikoala*, *Nimiokoala*, *Litokoala*, *Phascolarctos*) has a tendency to be bladed, as opposed to bicusped and weakly bladed in *Koobor*. Woodburne et al. (1987a) regard the bicusped P³ as plesiomorphic among phascolarctids but its occurrence in other vombatiform groups (e.g. ilariids and wynyardiids) suggests that it is apomorphic in phascolarctids.

2. *Trenchant P³*: *Phascolarctos* has a trenchant

P³ in contrast to a bulbous P³ in *Koobor*, *Madakoala*, *Perikoala* and *Nimiokoala*. Ilariids and wynyardiids have a bulbous, non-trenchant P³ suggesting the trenchant P³ in *Phascolarctos* is apomorphic.

3. *Posterobuccal cusp of P³*: The small posterobuccal cusp on P³ in *Koobor*, *Madakoala*, *Perikoala* and *Nimiokoala* is lacking in *Phascolarctos*. It is absent in wynyardiids and variable in ilariids. Its occurrence in most phascolarctids and ilariids suggests that it is plesiomorphic among phascolarctids.

4. *Crescentic paraconule*: The paraconule varies among phascolarctids from a small, linear structure in *Madakoala* and *Perikoala* to moderately developed in *Phascolarctos* (although not uniform), to a large crescentic paraconule in *Litokoala* and *Nimiokoala* occupying the longitudinal valley between the paracone and protocone. It is a moderate swelling at the anterolingual base of the paracone in M¹ of *Koobor*; however, it is suppressed on M²⁻³ as in ilariids. A paraconule is absent in wynyardiids but a small swelling at the anterolingual base of the paracone in ilariids. Hence, absence of a crescentic paraconule is regarded as plesiomorphic among phascolarctids.

5. *Neometaconule*: Absent in *Koobor*, weakly developed (or absent) in *Madakoala* and *Perikoala*, variable in *Phascolarctos*, large and crescentic in *Litokoala* and *Nimiokoala* (although reduced in the more posterior molars) and double cusped in the latter. Its absence is regarded as plesiomorphic in koalas because of its absence in ilariids and wynyardiids.

6. *Protostyle*: Present in *Phascolarctos*, *Nimiokoala* and *Litokoala* although it generally diminishes in size from M¹ to M⁴. It is absent in *Madakoala*, *Perikoala*, *Koobor*, ilariids and wynyardiids which suggests its presence is apomorphic.

7. *Stylar cusp development*: Large stylar cusps are thought to be primitive among

TABLE 4. Character state distribution within Phascolarctidae. Abbreviations: 0, plesiomorphic state; 1, apomorphic state; 2, more derived apomorphic state; ?, signifies missing data.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
<i>Phascolarctos</i>	1	1	1	0	1	1	1	1	1	1	1	2	1	1	1	1	0
<i>Litokoala</i>	1	1	1	1	1	1	1	1	1	1	2	2	1	1	1	1	1
<i>Nimiokoala</i>	1	0	0	1	1	1	1	1	0	0	2	2	0	1	1	0	1
<i>Perikoala</i>	1	0	0	0	1	0	1	0	0	0	0	1	0	0	1	0	0
<i>Madakoala</i>	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0
<i>Koobor</i>	0	0	0	0	0	0	0	0	0	0	1	?	?	?	?	?	?

diprotodontians (Rich & Archer, 1979), reflected in the enlarged styler cusps of ilariids and wynyardiids. Large styler cusps occur in *Koobor* and *Madakoala*. Although *Perikoala* has reduced styler cusps, the styler region is represented by a longitudinal crest that appears to subsume relatively large styler cusps. Those of *Nimiokoala*, *Litokoala* and *Phascolarctos* (excluding the parastyle of M^1) are suppressed relative to all other phascolarctids. Because of the large styler cusps in ilariids and wynyardiids, reduction in some phascolarctids is regarded as apomorphic.

8. *Posterolingual paracristae*: Well-developed and aligned with the preparacristae in *Nimiokoala*, *Litokoala* and *Phascolarctos* but absent (or weakly expressed) in *Koobor*, *Madakoala*, *Perikoala*, ilariids and wynyardiids. Absence is regarded as plesiomorphic.

9. *Cuspule at the anterolingual metaconular base of M^1* : A bulbous cuspule lies at the anterolingual base of the metaconule on M^1 of *L. kutjamarpens* (M^{2-4} unknown). It is variable in *Phascolarctos* but is absent in all other phascolarctids and ilariids and wynyardiids suggesting that absence is plesiomorphic.

10. *Anterolingual protocone crest of M^1* : An anterolingual crest extends from the apex of the protocone towards the base of the crown on M^1 of *L. kutjamarpens* and *Phascolarctos* resulting in a relatively square protocone base. This crest is absent in all other phascolarctids, in wynyardiids and in ilariids. Absence is regarded as plesiomorphic among phascolarctids.

11. *Parastylar development on M^1* : The parastyle ('styler cusp A') is regarded as a separate character (distinct from character 7) because it undergoes independent evolutionary change relative to styler cusps B through E. Small on M^1 of *Madakoala* and *Perikoala*; moderately developed in *Koobor*, *Litokoala* and *Phascolarctos*; large in *Nimiokoala*. The small parastyle of ilariids and wynyardiids suggests that this is the plesiomorphic condition.

12. *Protostylid*: The protostylid on M_1 has developed independently in pseudocheirids (Woodburne et al., 1987b), macropodoids (Archer, 1978a) and ilariids (Tedford & Woodburne, 1987). In koalas, the protostylid ranges from weak (*Madakoala*, *Perikoala*) to very large (*Nimiokoala*, *Litokoala*, *Phascolarctos*). Lower molars of *Koobor* are unknown. Because a protostylid is absent in wynyardiids (Pledge, 1987a) and probably ilariids (Tedford & Woodburne, 1987 consider both alternatives), a protostylid is interpreted here as derived.

13. *Metastylid fold*: An autapomorphy of the Phascolarctidae. *Phascolarctos* and *Litokoala* have a metastylid fold in which the post-metastylid cristid is continuous with the pre-entocristid. *Perikoala* and *Madakoala* lack the metastylid fold which is represented by a swelling at the posterior tip of the postmetacristid. *Nimiokoala* lacks a metastylid fold and the metastylid is reduced relative to other phascolarctids. Because it is absent in ilariids and wynyardiids it is difficult to determine polarity. However, considering that discrete metaconids and entoconids is the plesiomorphic condition in all marsupial groups, the condition within the Phascolarctidae in which these cusps are linked by blades, in this case via a metastylid, is interpreted as derived.

14. *Entostylid ridge*: Present in *L. kanunkaensis* and *Phascolarctos* and a well-developed cuspid in an homologous position in *Nimiokoala*. Its absence in the lower molars of ilariids and wynyardiids suggests that absence is plesiomorphic.

15. *Position of the protoconid on M_1* : Woodburne et al. (1987a) used this to determine koala intrafamilial relationships, with the more plesiomorphic koalas having a less lingual protoconid because of weaker protostylid development. The protoconid is within the lingual third of the trigonid of M_1 in *Perikoala*, *Nimiokoala*, *Litokoala* and *Phascolarctos*. Considering the buccal protoconid in wynyardiids and ilariids, the more lingual position in some phascolarctids is considered to be derived.

16. *Ribs on the conids of lower molars*: Internal ribs on the protostylid, metaconid, protoconid, entoconid and hypoconid of lower molars is apomorphic and shared by *Litokoala* and *Phascolarctos*. These ribs are absent in all other koalas. Presence is considered derived.

17. *Anteriorly displaced entoconid and anteriorly displaced metaconid of M_4* : Torsion of M_4 such that the entoconid is displaced anteriorly relative to the hypoconid and the metaconid is displaced anteriorly relative to the protoconid occurs in *Litokoala* and *Nimiokoala* but no other phascolarctids. This condition is absent in ilariids and wynyardiids; absence is interpreted plesiomorphic.

RESULTS

Wagner analysis using the branch and bound algorithm produced a single most parsimonious tree involving 22 steps with a CI of 0.864 and a RC of 0.746 (FIG. 7).

DISCUSSION

Recent classifications (e.g. Woodburne, 1984; Aplin & Archer, 1987) group the 6 fossil and living genera (14 species) of koalas in the Phascolaretidae; however, they also predict a large morphological range of koala-like animals. Woodburne (1984) erected the Superfamily Phascolaretoidea and Aplin & Archer (1987) the Infraorder Phascolaretomorphia, each containing only the Phascolaretidae. Complex molar morphology and plesiomorphic basicranial morphology of *Nimiokoala* indicate a more diverse infraorder of phascolaretomorphians.

In some aspects of dental morphology, *Nimiokoala* appears to have converged on pseudocheirids and ektopodontids. Slight torsion is evident in lower molars of *Nimiokoala* and the consequent arrangement of the metaconid and entoconid is similar to some pseudocheirids (e.g. *Pseudochiraps archeri*). Springer (1987) also noted more similarities in the M₄ of *L. kanunkaensis* to pseudocheirids than to any other phascolaretid. This is also the case with the M₄ of *Nimiokoala*.

Well-developed parastyle, large paraconule and large neometaconule of the upper molars of *Nimiokoala* and the entostylid ridge and neomorphic cusp on the lower molars are reminiscent of the cuspsate loph(id)s of ektopodontid molars; in particular the lower molars of *Darcus duggani* Rich, 1986 from the Pliocene Hamilton Local Fauna, Victoria. Archer (1976) suggested that the ektopodontid molar pattern may have evolved through an alignment of the wrinkles, conules and crenulations in the molars of selenodont forms and in particular, the koalas. The high crowned, highly crenulate, complex molars of *Nimiokoala* support this view.

Recent classifications (Archer & Aplin 1987; Marshall et al., 1989) support an ektopodontid/phalangerid affinity and place the Ektopodontidae within the Phalangerioidea based on the shared strongly angulate cristid obliqua and reduced metaconid on the lower molars and the loss of P1. Consequently, similarities in phascolaretid and ektopodontid molars suggest similar ecological niches. Pledge (1982) suggested several possible dietary preferences of ektopodontids, ranging from browsing and frugivorous to granivorous and insectivorous. Similar dietary specialisations could explain the complex dentitions of *Nimiokoala*.

Since the first fossil koala was described in 1957 there have been two different attempts to

analyse intrafamilial relationships. Archer (1978a) separated phascolaretids into *Litokoala*, *Koobor* and *Perikoala* Phascolaretos lineages. *Litokoala kutjamarpensis* was considered to be the most plesiomorphic phascolaretid based on the metaconule and lingual buttresses on the metacone of the upper molar (Archer, 1978a). *Perikoala* and *Phascolaretos* were interpreted to be more closely related to each other than either was to *L. kutjamarpensis*. However, Archer (1978a) also noted a large structural distance separating these groups. *Perikoala* exhibited a number of plesiomorphic features relative to *Phascolaretos* and several autapomorphic features that precluded it being antecedent to *Phascolaretos*. Molar morphology of *Koobor* led to its interpretation by Archer (1978a) as the sister-group of a combined *Phascolaretos*/*Perikoala* clade.

Woodburne et al.'s (1987a) cladistic analysis followed a reassessment of character state morphoclines for phascolaretids. Relative positions of *Phascolaretos*, *Litokoala*, *Perikoala* and *Mudakoala* are confirmed herein (Fig. 7). Relationships of *Litokoala* have been unclear due to its poor fossil record. Archer (1978a) regarded it as the plesiomorphic sister group of all phascolaretids based on a single upper molar. Re-analysis of that tooth by Woodburne et al. (1987a) and Springer's (1987) 2 isolated lower molars and upper molar fragments of *L. kanunkaensis* suggested *Litokoala* was more closely related to *Phascolaretos*. *Litokoala* material from Riversleigh supports Woodburne et al.'s (1987a) hypothesis.

Features now found to support the *Litokoala* and *Phascolaretos* relationship include the neomorphic cuspule at the anterolingual base of the metaconule on M¹ (and M²⁻⁴ in *Phascolaretos*), the metastylid fold in which the postmetastylid cristid is a continuous fold with the preentoeristid and the internal ribs on the cusps of lower molars. Features, regarded by Springer (1987) as autapomorphies of *L. kanunkaensis* but which are in fact variably present in *Phascolaretos* include anteriorly bifurcate pre-entoeristid, reduced talonid on M₄ and parallel arrangement of the cristid obliqua and postprotoeristid on M₄ wherein these cristids do not meet end to end. The latter two features are also variably present in *Nimiokoala*. *Litokoala* is a derived relative to *Phascolaretos* in having a more crescentic paraconule and neometaconule in the upper molars, a well-developed metaconid

posterobuccal crest on M_{2,4} and in having a well-developed posterolingual protoconid on M₄.

Nimiokoala, *Litokoala* and *Phascolarctos* form a clade by sharing a protostyle in the upper molars, strong posterolingual paracristae, a large protostylid on M₁ and a well-developed entostylid ridge. *Litokoala* and *Nimiokoala* are derived relative to *Phascolarctos* in the shared crescentic paraconule and neometaconule in M¹⁻⁴ and a well-developed parastyle on M¹. *Litokoala* and *Nimiokoala* synapomorphies, interpreted as convergences (Fig. 7) are: well-developed, highly crescentic paraconule and neometaconule, large, pyramidal parastyle and extreme torsion on M₄ such that the entoconid and metaconid are displaced anteriorly relative to the hypoconid and protoconid, respectively. *Nimiokoala* is derived relative to other phascolarctids in having strong posterobuccal crests from the apices of the protocone and metaconule, a discontinuous neometaconule which is subdivided into two cusped parts, a posterolingual cuspule on P², a well-developed posterolingual protostylid cristid on M₁, weak metastylid in the lower molars, an anterobuccally directed preentocristid (anterolingually directed in other phascolarctids) and a neomorphic cuspid occupying the trigonid basin between metaconid and protoconid on M_{2,4}.

There are doubts about the inclusion of *Koobor* in Phascolarctidae. Pledge (1987b) suggested that *Koobor* is allied to ilariids such as *Kuterintjanguama*. Figure 7 may support the hypothesis that it lies outside the Phascolarctidae. Clarification of *Koobor*'s relationships requires discovery of lower molars because these differ significantly in ilariids and phascolarctids.

Except for 2 partial skulls from Riversleigh, extinct phascolarctids are represented by isolated teeth or dentitions. As a result, current understanding of the basicranial region is based on the modern species. *Phascolarctos cinereus* has an autapomorphic bilaminar bulla wherein the tympanic cavity is roofed by both an alisphenoid tympanic process and the squamosal epitympanic wing (Aplin, 1987). The partially preserved basicranial region of *Nimiokoala greystanesi* (Fig. 1A-C) exhibits the plesiomorphic diprotodontian condition wherein the alisphenoid forms the roof of the tympanic cavity, suggesting a large structural distance between these koalas. The plesiomorphic basicranium of *N. greystanesi* supports the hypothesis that phascolarctids diverged from near the base of the diprotodontian tree (Archer, 1976).

Intragenetic relationships of *Litokoala* are dif-

ficult to interpret due to a lack of comparable material between the species. *Litokoala kanunkaensis* appears to be plesiomorphic relative to *L. kutjamarpensis* because it lacks a proto style and the bulbous cuspule at the anterolingual base of the metaconule on M³. However, these features may be a result of changes along the tooth row (ie. an artefact of comparing an M³ with an M²), rather than interspecific differences.

Litokoala kanunkaensis from early-middle Miocene System C (Archer et al., 1989; 1991) is the same age or slightly younger than, the Kutjamarpu Local Fauna.

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